Threats to North American forests from southern pine beetle with warming winters

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In coming decades, warmer winters are likely to ease range constraints on many cold-limited forest insects[1–5]. Recent unprecedented expansion of the southern pine beetle (SPB, *Dendroctonus frontalis*) into New Jersey, New York, and Connecticut in concert with warming annual temperature minima highlights the risk that this insect pest poses to the pine forests of the northern United States and Canada under continued climate change[6]. Here we present projections of northward expansion in SPB-suitable climates using a statistical bioclimatic range modeling approach and current-generation general circulation model (GCM) output under the Representative Concentration Pathway (RCP) 4.5 and 8.5 emissions scenarios. Our results show that by the middle of the 21st century, the climate is likely to be suitable for SPB expansion into vast areas of previously unaffected forests throughout the northeastern United States and into southeastern Canada. This scenario would pose a significant economic

26   **and ecological risk to the affected regions, including disruption of local ecosystem**

27   **services[7], shifts in forest structure[8], and threats to native biodiversity[9].**

28   SPB is a major forest pest in the southeastern United States responsible for 14 million

29   m^3 of timber losses worth an estimated US$1.7 billion over 1990-2004[10]. SPB has historically

30   been most damaging in southeastern states, with limited activity in the northern portion of

31   its range including Ohio, Pennsylvania, and Maryland. However, SPB outbreaks have become

32   increasingly problematic and extensive in southern New Jersey since 2001, and populations

33   have been detected for the first time on Long Island, New York, in 2014 and in Connecticut

34   in 2015[6,11].

35   A link between SPB outbreaks and winter cold extremes has long been recognized[12],

36   and minimum air temperatures between -14 and -20ºC have been observed to cause critical

37   overwintering mortality in SPB[4,13,14]. The recent northward expansion of SPB has occurred

38   amidst regionally warming winters and decreasing incidences of cold extremes[15]. Since

39   mean annual temperatures in the northeastern United States are projected to rise by 2-6ºC

40   by 2100[15], with possibly larger increases in winter cold extremes[16,17], the climatic

41   constraints limiting SPB incursion further into northern pine forests will likely recede

42   dramatically in the coming decades. Here we present a projected timeline for the expansion

43   of SPB-suitable climates in eastern North America under continued climate change through

44   2090.

45   Previous modelling experiments of SPB range expansion under climate change have

46   used statistical and physiological relationships between SPB outbreaks and weather

47   established within the historic range, assuming that these relationships hold at the

48   expansion frontier, and have applied uniform climatic perturbations that overlook the

49   temporal complexity and spatial heterogeneity of projected warming[4,5]. In this study, we

50   address these shortcomings by developing a statistical model linking recent SPB range

51   expansion to changing incidence of cold extremes, and by using spatially-explicit current-

52   generation GCM projections.

53   We also robustly analyze the sources and magnitudes of uncertainty in this timeline

54   of expansion. In climate prediction, there are generally three components of total

55   uncertainty: *internal variability* (natural stochastic climate variability), *inter-GCM variability*

56   (resulting from differences in construction between GCMs), and *scenario uncertainty* (due to

57   variation between plausible future emissions scenarios). Our phloem temperature model,

58   which simulates thermal inertia of tree stems, introduces an additional source of uncertainty

59   related to the thermal buffering coefficient, the K-value, which depends on tree diameter (*see*

60   Methods). Uncertainty estimation in past projections of insect range expansion under

61   climate change has examined only variable emissions scenarios, ignoring other sources of

62   uncertainty[1-3]. While inter-model variability and scenario uncertainty are technically

63   reducible, internal variability is fundamentally irreducible and therefore defines the

64   theoretical minimum uncertainty in estimated timelines of SPB-suitable climate expansion

65   (*see* Supplementary Information). In this study, we estimate the proportion of total

66   uncertainty in our projections arising from various sources to understand its potential

67   reducibility and role in informing adaptive management decisions (e.g. prescribed fire, forest

68   harvesting[18]).

69   SPB's spread across southern New Jersey has occurred amid a warming trend: for

70   example, the -10°C winter minimum phloem temperature isotherm has migrated

71   northwards by 0.6° latitude (~65km) per decade since 1980 ($P<0.01$) (Fig. 1a). Meanwhile,

72   the latitude of the northernmost SPB sighting has drifted north by 0.8º latitude (~85km) per

73   decade since 2002 (*P*=0.01). Inter-annual north-south variation in SPB's northern range

74   frontier only weakly correspond to extreme temperature minima (Fig. 1a) and likely depend

75   on ecological factors of less consequence to longer-term changes including forest conditions,

76   host-tree vigor, and predator dynamics[19]. SPB is absent in all New Jersey grid cells

77   experiencing phloem temperatures less than -16ºC (corresponding to air temperatures of -

78   18 to -20ºC) (Fig. 1b), substantiating a lethal minimum temperature constraint on SPB. Our

79   estimate of this limiting temperature concurs with past estimates within SPB's historical

80   range[4], suggesting that recent range expansion is because of warming and not plasticity in

81   the cold tolerance of northern SPB populations[13].

82   Among a series of candidate range-predicting minimum phloem temperatures, we

83   found that the latitude of the -10ºC-isotherm best correlated with the latitude of the

84   northernmost SPB occurrence across 6 longitudinal bins (r^2 = 0.34, Fig. 1c, Supplementary

85   Fig. 2, Supplementary Table 3). This temperature exceeded the lethal limit of -16ºC, likely

86   because low beetle survival at or below -16ºC reduced the likelihood of a sighting. We

87   therefore designated the year after which winter minimum phloem temperatures remain

88   above -10ºC for ten consecutive years as the year of emergence of a SPB-suitable climate.

89   This ten-year window can be applied consistently to each annual time step over 2006-2080

90   (*see* Supplementary Information).

91   Based on the 27-GCM mean (Supplementary Table 1), we project increases in annual

92   minimum air temperature of 3.5-7.5ºC for RCP 4.5 and 8.5 across the northeastern United

93   States and southeastern Canada by 2050-2070, with annual minimum phloem temperatures

94   rising by a slightly smaller 3.0-7.0ºC (Supplementary Fig. 3). These projections are consistent

95   with other studies using CMIP5[16] and other model suites[17]. Given this warming trend and

96   our criteria for SPB-suitable climates, vast areas across the northeastern United States and

97   southern Ontario and Quebec are projected to become climatically hospitable to SPB

98   populations before 2080 (Fig. 2a), according to multi-run mean projections. We project

99   sufficient warming for the establishment of SPB along the Atlantic coast to Nova Scotia before

100 2020, and from southern New England through Wisconsin between 2040 and 2060 (Fig. 2a).

101 The projected years of emergence for areas already affected by SPB in New Jersey and New

102 York agree with observations. These results are relatively robust to alternative range-

103 predicting temperatures (Fig. 3, *see* Methods).

104   There is considerable uncertainty in the above multi-run mean results. Among 162

105 model runs using differing GCMs, emissions scenarios, and *K*-values (*see* Methods), the

106 earliest projected year of emergence differs from the latest by 43 years (Fig. 2b-c). To

107 understand the origin of this uncertainty, we estimated the proportion of total uncertainty

108 arising from the four sources (Fig. 4a): internal variability (12%), emissions scenario (13%),

109 inter-GCM (58%), and *K*-value (17%). While uncertainty from internal variability is

110 theoretically fully irreducible and comprises a plurality of total uncertainty in some areas

111 (Fig. 4b), the emissions scenario and inter-GCM portions are effectively irreducible in the

112 near term (*see* Supplementary Information). This finding suggests that forest managers

113 should consider the range of plausible years of emergence in setting adaptation priorities

114 and strategies.

115   In addition to sufficiently mild winters, SPB requires suitable host tree species with

116 sufficient areal density to survive in a given location. To identify where and when SPB-

117 suitable climates coincide with SPB-susceptible forests, we mapped the ranges of forest

types defined by dominant pine species alongside isolines representing multi-run mean years of SPB-suitable climate emergence across the study region (Fig. 5a). These forest type ranges are expected to shift under climate change[20], but because projected changes in dominant species are small through 2100[21], we approximated them as static in our analysis. We also mapped the basal area density of the various pine species over the study region to identify pine-sparse areas that may inhibit further SPB spread (Fig. 5b).

By 2050, 78% of the 124,000 km^2 range of pitch pine (*Pinus rigida*) forests extending from southern Maine to eastern Ohio are projected to feature newly-SPB suitable climates. This forest ecosystem is particularly vulnerable to SPB and has already suffered unprecedented widespread tree mortality in New Jersey and New York[6,11]. Our projections demonstrate a significant risk to pitch pine forests within 35 years, including broad disruption of local ecosystem services[7], shifts in forest structure[8], and threats to native biodiversity[9].

By 2080, we project that SPB-suitable climates will reach 71% of the red pine (*P. resinosa*) and 48% of jack pine (*P. banksiana*) forest ranges that extend across more than 706,000 km^2 in the northeastern United States northwards through subarctic Canada (Fig. 5a). It is uncertain whether SPB will thrive in forests dominated by these pine species. However, SPB is highly polyphagous among pine species in its historical range[22], and tree attacks have recently been documented for the first time in red and white (*P. strobus*) pines on Long Island, New York and Connecticut (personal communication). Although successful reproduction of SPB in white pine has not yet been documented, a moderate density of more suitable pitch and red pine across the region may provide a pathway for expansion (Supplementary Fig. 6, *see* Supplementary Information).

141   Pine-sparse hardwood forests in the northern United States may present a barrier to

142   continued SPB dispersal into the red and jack pine forests further north. However, SPB has

143   already traversed large pine-sparse regions in the eastern United States, and forests further

144   north feature a higher, more continuous density of pine (Fig. 5b). The Great Lakes pine

145   forests are separated to the south and east by a larger pine-sparse zone. Our projections

146   indicate that the pine-dense Canadian forests north of the Great Lakes will become

147   climatically suitable by 2050-2080, opening a plausible route for SPB spread to these forests

148   (Fig. 5a).

149   Although SPB has already been detected in western Connecticut in 2015, we project

150   these areas to be climatically suitable for SPB only after 2025. Long range SPB dispersal is

151   poorly understood[23] and may occur over greater distances than previously thought[24] (e.g.

152   2010, Fig. 1a). These earlier-than-predicted sightings could reflect a tendency of SPB to

153   disperse far beyond its climatically-constrained range[22], as observed in New Jersey in 2014

154   (Fig. 1a), but fail to survive a subsequent winter and establish stable populations. In this case,

155   our model might accurately project longer-term range expansion despite omitting shorter-

156   term leaps. By contrast, sustained future SPB presence in these areas would suggest that our

157   model underestimates the pace of expansion. Continued SPB monitoring will enable a

158   rigorous assessment of this aspect of our model's performance and further research into the

159   relationship between long-term and intermittent range expansions.

160   Further ecological and climatological factors not simulated in our study, such as

161   drought, fire, and community-level interactions, may affect future SPB range expansion. By

162   mid-century, the northeastern United States is likely to experience elevated drought risk and

163   10-40 additional extreme heat days per year[15]. Some forest types are more susceptible to

164   attack by bark beetle when stressed by drought and extreme heat[25]; however, the link

165   between drought and SPB may be weaker[26] or more nuanced[27] than for other beetle species.

166   In contrast to some conifer-infesting beetles, SPB has not been strongly linked to natural or

167   prescribed fire[28]. However this association may become clearer if fire regimes shift under

168   climate change. Although SPB may encounter suppression by or release from predators and

169   competitors in newly suitable areas, SPB's primary predator (*Thanasimus dubius*) is widely

170   distributed in eastern North America[29] and has not strongly influenced recent expansion.

171   Finally, while our analysis projects future change in SPB-suitable areas, the degree of SPB

172   damage to forests depends on outbreak intensity, which is linked to climate, forest

173   conditions and management, and SPB population dynamics[18]. Further monitoring and

174   research are needed to understand how these factors may affect the regional impacts of SPB

175   into the future (*see* Supplementary Information).

176   Our study reveals a plausible new threat from SPB to vast areas of pine forest in

177   eastern North America by 2050 and into subarctic Canada after 2080 under continued

178   climate change. Meaningful global greenhouse gas emissions mitigation can reduce the

179   projected risks only after 2050, as projected warming is largely independent of emissions

180   scenario for the coming few decades[30]. Further monitoring and research concerning the

181   additional determinants of SPB range not simulated in our projections, such as the suitability

182   of northern pine species and the role of drought, will improve the understanding of SPB's

183   implications for northern pine forests. Despite these uncertainties, our results suggest that

184   the mounting threat posed by SPB to regional ecosystems, biodiversity, and economies is

185   likely to become increasingly relevant to forestry managers and policy makers as climate

186   change proceeds.

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273   **Supplementary Methods** is linked to the online version of the paper.

282   **Author contribution.** C.L. and E.C. conceived and coordinated this research and performed

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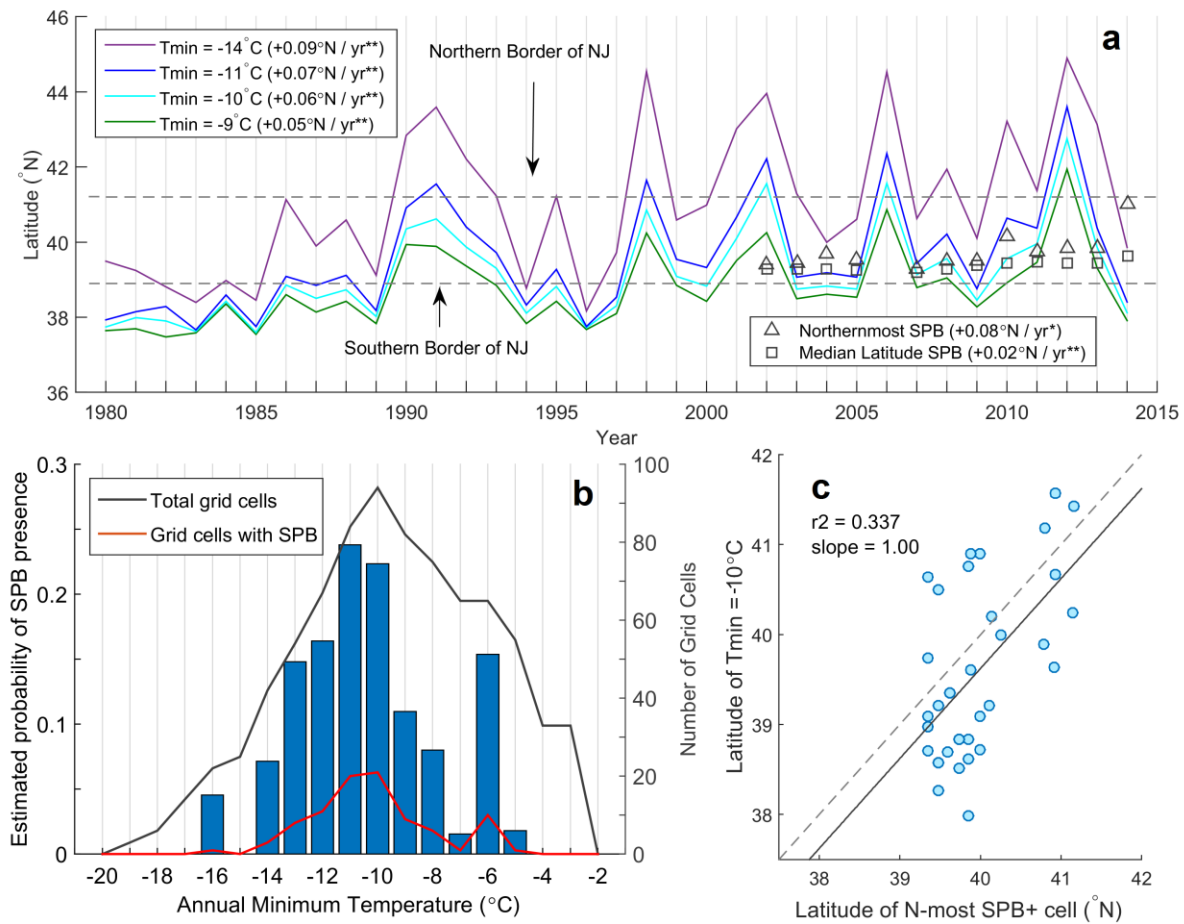
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Figure 1: Spatial correspondence between recent SPB expansion and warming annual minimum phloem temperatures. (a) Southernmost latitudes of occurrence for various minimum winter phloem temperatures over 1980-2014 (solid lines), maximum (triangles) and median (squares) latitude of SPB presence across New Jersey over 2002-2014 (no data for 2006). Linear trends in latitudes are shown in legends (double asterisks denote P<0.01, single asterisks denote P<0.05). (b) Total cells (black line), cells with SPB presence (red line), and estimated probability of SPB presence (bars) over 1°C annual minimum phloem temperature bins. Data are aggregated across New Jersey over 2002-2014. (c) Latitude of northernmost SPB-positive grid cell versus southernmost latitude of critical phloem temperature at corresponding longitudes over 2002-2014 for the range-predicting temperature of -10ºC (n=36). The one-to-one relationship is shown in dashes.
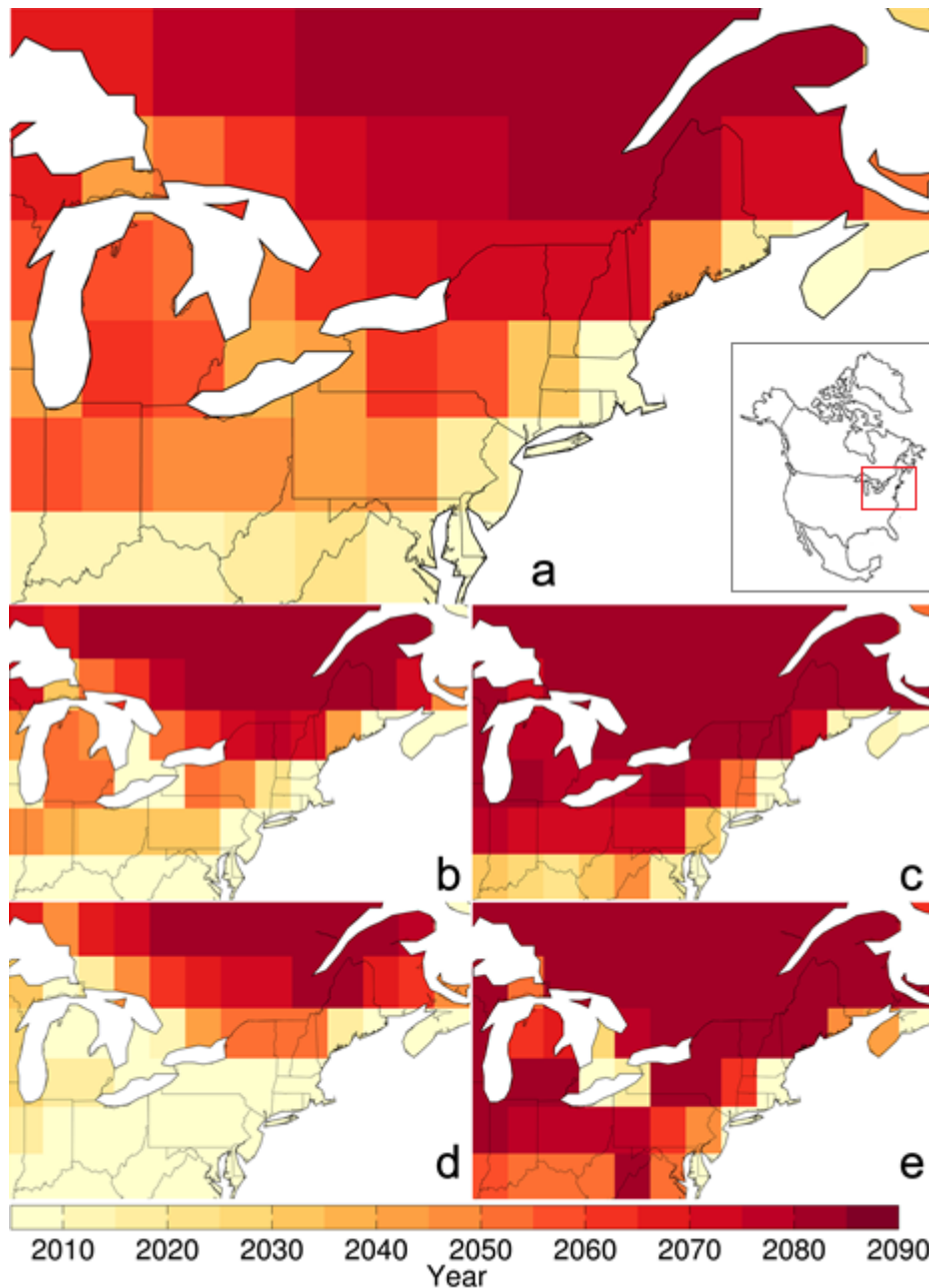
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Figure 2: Projected year of emergence of an SPB-suitable climate, defined as the year for which minimum phloem temperature of -10°C is not reached in the following decade. (a) mean of full set of 162 model runs (27 GCMs, two emissions scenarios, and three K-values); (b) 25th percentile of the full set; (c) same as (b) but for the 75th percentile; (d) minimum of internal variability range across 60 runs (10 CSIRO-MK3 ensemble members, two emissions scenarios, and three K-values); (e) same as (d) but for the maximum.
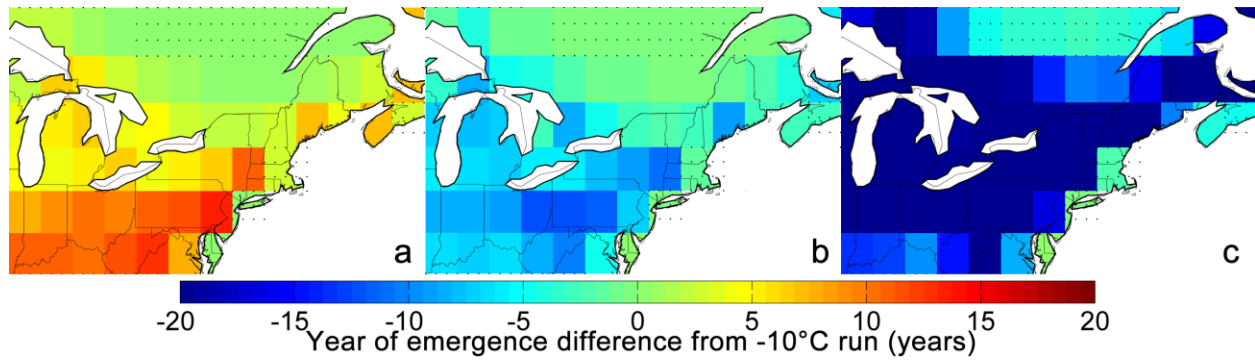
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Figure 3: Projected year of emergence of SPB-suitable climate using alternative definitions of SPB-suitability. Next-best range-predicting temperatures of (a) -9°C and (b) -11°C, and (c) the lethal temperature of -16°C. Results are presented as differences compared to main results using -10°C (Figure 2). Stippling indicates grid cells for which results are highly robust (difference <5 years across all alternative definitions).
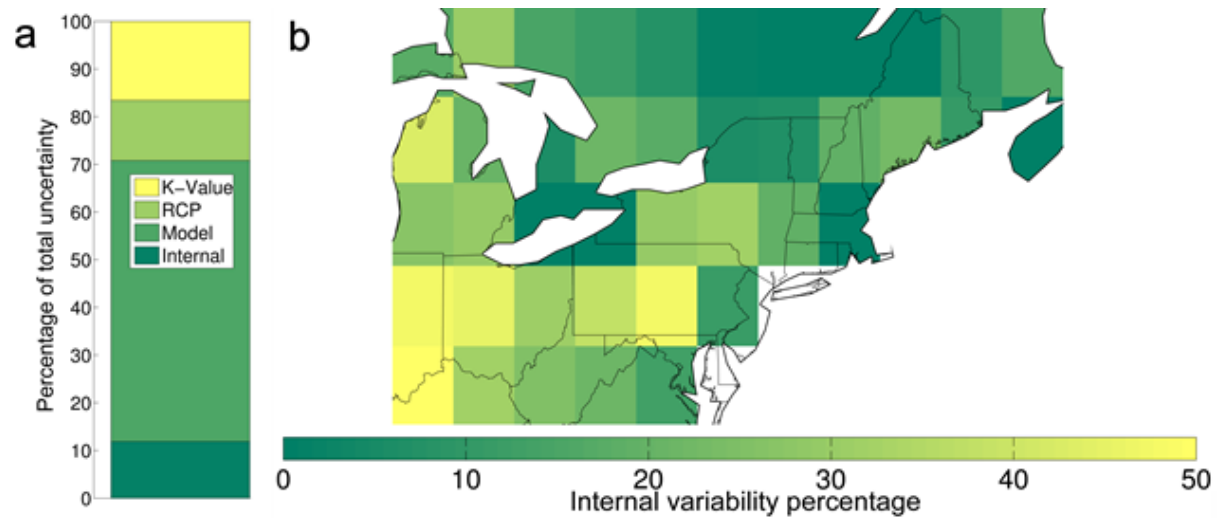
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Figure 4: Drivers of uncertainty in projected year of emergence of SPB suitable climates. (a) Estimated partitioning of total year of emergence uncertainty into its four components: internal variability (dark blue), differences between GCMs (light blue), emissions scenarios (RCP, green), and *K*-values (yellow). (b) Estimated percentage of the total uncertainty resulting from internal variability across the study region, ranging from 10-50% among non-coastal grid-cells. Although reduction of all sources of uncertainty is technically challenging, uncertainty due to internal variability is theoretically irreducible and therefore unavoidable in setting adaptation priorities and strategies (*see* Supplementary Information).
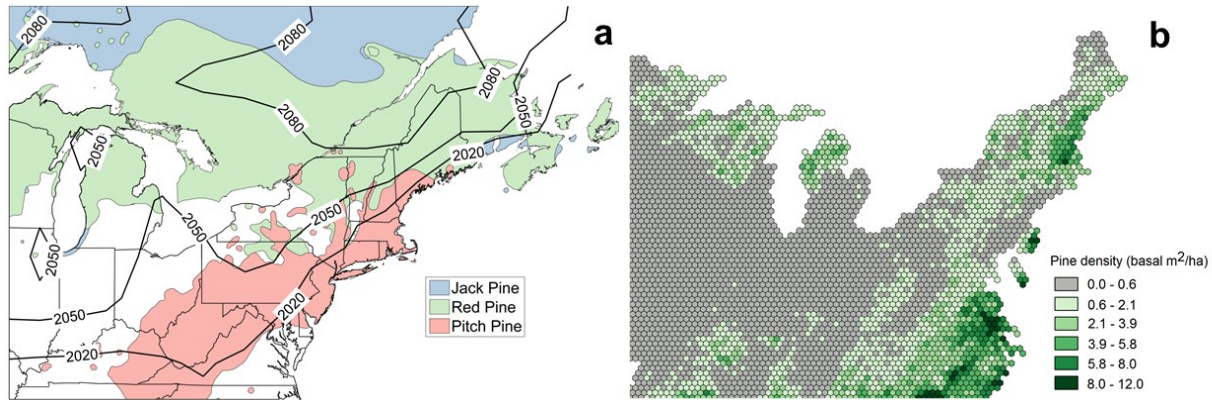
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Figure 5: Projected SPB expansion into ranges of forests with suitable dominant pine species. (a) Lines of equal year of emergence of SPB-suitable climate (black lines) and ranges of forest types defined by dominant pine species across the northeastern U.S. and southeastern Canada. Climates suitable for SPB are projected to reach 78% of previously unaffected North American pitch pine (red, *Pinus rigida*) forests by 2050, and 71% of red pine (green, *P. resinosa*) and 48% of jack pine (blue, *P. banksiana*) forests by 2080. (b) Aggregate basal area density (m²/ha) of selected *Pinus* species across the northeastern United States. SPB has already dispersed across large areas of low pine density along its expansion trajectory.

Methods

The dynamics of phloem heating and cooling in response to winter temperature variation is an important determinant of the minimum winter temperature that an overwintering SPB is exposed to. To simulate the thermal buffering of tree stems, we modeled phloem temperatures using a linear Newtonian heat flux model with thermal buffering coefficient values (*K*-values) representative of regional forest structure[14]. This phloem temperature model was used for both historical and projected future temperatures.

For the historical portion of our analysis, we drove the phloem temperature model using bias-corrected historical air temperature data with 30km grid resolution at 3-hourly intervals from North American Regional Reanalysis[31] (*see* Supplementary Information). To identify the critical minimum phloem temperature for SPB in New Jersey, we mapped the presence or absence of SPB based on aerial pest detection surveys over 2002-2014[32] (data missing for 2006) onto the annual minimum phloem temperature grids. We then estimated the probability of SPB occurrence at minimum temperatures ranging from -20 to -2°C as the number of cells with SPB divided by the total number of cells with given minimum temperature. The probability of SPB occurrence dropped to 0 for all temperatures less than -16°C, indicating a lethal minimum temperature.

To select the phloem temperature that best predicted the northern range limit of SPB, we assessed a window of 7 candidate temperatures (-8 through -14°C) centered on the temperature of peak probability of SPB occurrence (-11°C). We collated 36 annual grid cells with active SPB populations across 6 longitudinal bins and for each cell observed the southernmost latitude at which each of seven candidate critical temperatures occurred at the cell's longitude (to account for varying climates from coastal to interior New Jersey). We then fit linear trends to scatter plots of the latitude of northernmost SPB populations versus latitudes of the candidate minimum temperatures (Supplementary Fig. 2). A linear regression with slope of one, intercept of zero, and r^2 of one would indicate perfect correspondence in space between the northern limit of SPB range and southernmost occurrence of that candidate minimum temperature (*see* Supplementary Information). We found that the critical temperature of -10°C best matched these criteria, with slope of 1.00, $r^2 = 0.34$, and an intercept of ~0.4° of latitude (Fig. 1c, Supplementary Fig. 2, Supplementary Table 3, *see* Supplementary Information). Two other candidate temperatures (-9°C and -

368   11ºC) satisfied these criteria nearly as well, so we treated them as alternate plausible range-

369   predicting temperatures in the sensitivity analysis.

370   Future daily phloem temperatures over 2006-2090 were projected independently for

371   27 CMIP5 GCMs[33] under the RCP 4.5 and 8.5 emissions scenarios[34] (Supplementary Table 1)

372   in conjunction with the phloem temperature model. Model-specific mean temperature biases

373   due to factors such as varying parameterization schemes and internal model dynamics

374   ranged from 3-5ºC relative to the NCEP reanalysis[35]. To correct these biases, we divided the

375   daily maximum and minimum temperature distributions for NCEP reanalysis and each

376   model into ten 10-percentile bins and corrected the mean bias between the model and the

377   reanalysis for each bin[17] (Supplementary Fig. 4). This method accounts for generally larger

378   bias near the high and low tails (Supplementary Fig. 5). Residual biases were minimal except

379   on the periphery of the study area.

380   Year of emergence of an SPB-suitable climate was estimated as the first year in which

381   the critical minimum temperature of -10ºC was not reached in the following decade. This ten-

382   year window was chosen as it could be applied consistently to each annual time step over

383   2006-2080. We present the mean year of emergence across all -10ºC runs in Fig. 2a. To

384   examine the sensitivity of these multi-run mean results to varying plausible definitions for

385   the emergence of SPB suitability, we recomputed the year of emergence projections for the

386   next-best range predicting temperatures of SPB's northern frontier (-9ºC and -11ºC, Fig. 3a-

387   b). We also examined the results using the lethal minimum temperature of -16ºC[13] (Fig. 3c,

388   Supplementary Information). The alternate results (Fig. 3) are presented as differences in

389   the multi-run mean year of emergence from the -10ºC result in Fig. 2a. Projections using the

390   next-best predictors of SPB's northern frontier (-9ºC and -11ºC, Fig. 3a-b) differed from those

391   under the -10ºC definition by ≤2 years on region-wide average, indicating low sensitivity of

392   the results to alternative range-predicting temperatures. Projections based on the lethal

393   minimum temperature (-16ºC, Fig. 3c)[13,14] as opposed to the range-predicting temperatures

394   were 14 years earlier on region-wide average; these results may be considered an earliest

395   plausible projected timeline of SPB emergence (*see* Supplementary Information).

396   Total uncertainty in the year of emergence projections was estimated by considering

397   the full set of 162 model runs generated from the combination of 27 CMIP5 GCMs, two

398   emissions scenarios (RCP4.5 & 8.5), and three K values. We presented the 25th and 75th

percentiles of this full set as the central range of year of emergence results (Fig. 2b-c). To estimate the partitioning of the total uncertainty into its constituent sources, we employed two different methods. For the emissions scenario, GCM, and *K*-value sources, we estimated the percentage of uncertainty arising from each source as its year of emergence range over the year of emergence range of the full set (*see* Supplementary Information). For internal variability, we applied a similar method using a suite of 60 results based on a 10-member ensemble of the CSIRO-MK3 GCM[36] driven by the 2 emissions scenarios and 3 *K*-values (Fig. 2d-e). We present these rescaled partitioned uncertainties in Fig. 4a, along with a map of the internal variability ratio in Fig. 4b (*see* Supplementary Information).

Lines of equal year of emergence were fit to the multi-run mean year of emergence maps and were manually smoothed in some areas to reduce implausible precision induced by the contour fitting algorithm, especially near coastal grid cells (Fig. 5a). Data on the spatial extent of pitch, red, and jack pine forests was obtained from the US Forest Service Forest Inventory and Analysis Program (Fig. 5a)[37], and we mapped basal area density of pine species using a derived raster imputation basal area map also from the US Forest Service (Fig. 5b)[38]. The area of forest newly climatically suitable for SBP was calculated as the suitable area in 2050 (for pitch pine) or 2080 (for red and jack pine) minus the suitable area in 2007 (no jack or red pine forests were suitable for SPB in 2007).

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